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VARIATION IN THE BOUNCE AND WHINNY SONGS OF THE EASTERN SCREECH-OWL

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ABSTRACT.—Intra- and interindividual variation in the "bounce" and "whinny" songs of Eastern Screech-Owls (*Otus asio*) in central Kentucky were examined. Significant interindividual variation was noted in each character examined. Temporal characters generally were more variable than frequency characters in "whinny" songs, but the reverse was found to be true for "bounce" songs. Interindividual variation was also noted in the structure of notes used in "bounce" songs. The "bounce" songs of females were significantly longer in duration and higher in frequency than those of males. Our results suggest that there is sufficient variation in these songs to permit sexual and individual recognition. *Received 20 Jan. 1987, accepted 6 May 1987.*

The song repertoire of Eastern Screech-Owls (*Otus asio*) includes the "whinny" (primary song) and the "bounce" (secondary song). Previous investigators have reported both individual and geographic variation in these songs. Lynch and Smith (1984) noted that differences in the frequency of songs could be used to determine if owls being surveyed were new or had been counted previously. Andrews et al. (1982), using playback to count Eastern Screech-Owls in Massachusetts, reported that responding owls exhibited considerable variation in the frequency of the tremolo ("bounce" song). Marshall (1967) reported regional variation in the "whinny" song. Here we examine intra- and interindividual variation in the "bounce" and "whinny" songs of Eastern Screech-Owls in central Kentucky.

METHODS

Recordings of 24 Eastern Screech-Owls were made from 21 May to 3 July 1984 and from 16 June to 20 August 1985 in Madison County, Kentucky. Most recordings were made at the Central Kentucky Wildlife Management Area, 17 km SSE of Richmond, Kentucky. Additional recordings were made in an area 3.7 km SSW of Richmond. All recordings were of songs uttered in response to the playback of "bounce" and "whinny" songs. Playback tapes were made using (1) recordings of screech-owls obtained in the study area and (2) owl songs in "A field guide to bird songs of eastern and central North America" (Anonymous 1975). Recordings were sometimes obtained during and after playback experiments performed in conjunction with another study (Cavanagh 1986). During these experiments the "bounce" songs of neighboring and nonneighboring owls were played for 5 min. On other occasions songs were broadcast for as long as 15 min.

Eight owls were captured and fitted with radiotransmitters to aid in individual identification. Transmitters were attached backpack style (Smith and Gilbert 1981) using nylon

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TABLE 1
VARIATION IN NINE VARIABLES OF "BOUNCE" SONGS

Variable	N[a]	Minimum	Maximum	Mean	SD	CV
Notes/song	22	25.10	39.74	32.30	3.42	10.59
Duration (sec)	22	1.70	2.66	2.30	0.24	10.30
Notes/sec	22	12.71	15.00	14.05	0.68	4.87
Initial frequency[b]	20	364	949	723	124	17.10
End frequency	20	398	944	721	115	15.99
Maximum frequency	20	441	999	754	120	15.89
Minimum frequency	20	364	929	708	117	16.53
Frequency range	20	19	76	48	15	31.68
Mean frequency	20	414	983	735	120	16.27

[a] N = number of individuals. For the first 3 variables, 411 songs were analyzed (range = 7–30 songs/individual). For all frequency variables, 200 songs were analyzed (10 songs/individual).
[b] All frequency measurements in Hertz.

cord. Owls were captured by (1) taking them from nest boxes or natural cavities or (2) luring them into a mist net using playback of "bounce" songs. The sex of several captured owls was determined by (1) the presence or absence of an incubation patch and (2) behavior during the nesting season. During this time, females generally roost in nest cavities (either incubating eggs or brooding nestlings) while males often roost in nearby trees (pers. obs.).

Owls with transmitters were often recorded on several different occasions, sometimes over a period of more than a year. Recordings of owls without transmitters were obtained once at one location.

All recordings were made using a Uher 4000 Report Monitor tape recorder at a tape speed of 4.7 or 9.5 cm/sec with a Dan Gibson parabolic microphone. Songs were analyzed using a Kay Elemetrics Co. Sona-Graph (Model 6061A) at the wide band-pass setting. Measurements of the duration of entire songs, individual notes, and internote intervals were made using a ruler. A note was defined as a continuous trace on a sonagram. Frequency measurements were made to the nearest 25 Hz using a transparent overlay. All analyses were performed using the Statistical Analysis System (SAS Institute 1985) General Linear Model for unbalanced data.

RESULTS

"Bounce" songs are composed of a series of notes repeated at a constant or nearly constant frequency (Fig. 1A, B) (Table 1). The mean duration [±SD] of individual notes was 30.32 ± 6.06 msec (N = 5982) while the mean internote interval was 25.01 ± 3.79 msec (N = 5796) in duration. The duration of successive notes within bounce songs differed significantly ($F = 93.34$, $P < 0.001$). Typically, the duration of successive notes increased in the first part of a song, peaked, then decreased (Figs. 1, 2). The longest note in a typical bounce song was 1.86 times as long (N = 20 owls, Range = 1.55–2.50) as the shortest note. The duration of successive internote intervals also varied within songs ($F = 52.39$, $P < 0.001$).

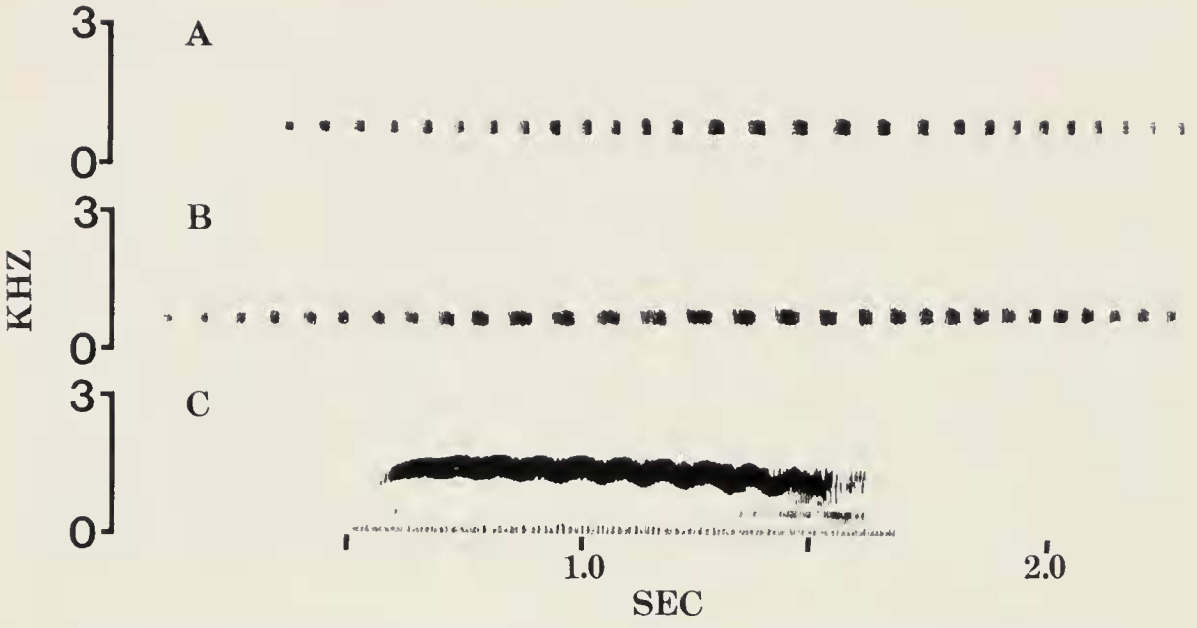

FIG. 1. The "bounce" (A, B) and "whinny" songs (C) of Eastern Screech-Owls.

Internote duration typically was longer at the beginning and again at the end of a "bounce" song (Figs. 1A, B; 2). Individual differences were observed in the pattern of variation for both note and internote duration (Fig. 3). For all owls combined (N = 20) the note with the longest duration was note 15 (Fig. 2); however, among individuals the note with the longest duration ranged from note 5 to note 25 (Fig. 3). Although the internote duration was generally longest at the very beginning of a "bounce" song, a second peak in internote duration was always observed. This second peak corresponded to the peak in note duration (Fig. 2).

Much interindividual variation in "bounce" songs was apparent. One-way analysis of variance revealed significant individual differences ($P < 0.001$) for every parameter examined, with frequency variables exhibiting more interindividual variation than temporal variables (Table 1). Within individuals, frequency was relatively constant while temporal variables (duration and number of notes per song) exhibited more variation. A comparison of coefficients of variation indicated that intraindividual variation was consistently less pronounced than interindividual variation.

Interindividual variation in note structure was also observed (Fig. 1A, B). Individual owls consistently uttered notes with the same structure. Two individuals that we recorded over a period of more than one year showed no change in the structure of "bounce" song notes.

Significant differences were observed in the "bounce" songs of male (N = 5) and female (N = 3) screech-owls (Table 2). The "bounce" songs of females were significantly longer in duration and higher in frequency

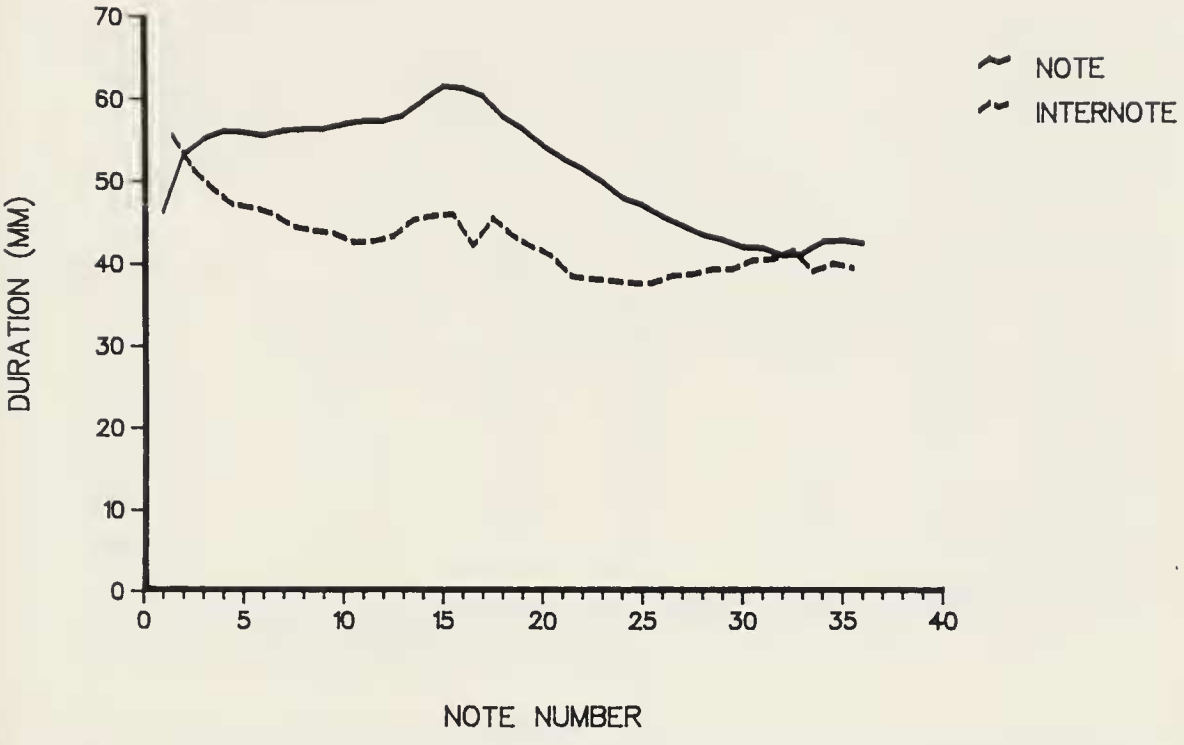

FIG. 2. Mean note and internote durations in the "bounce" songs of 20 Eastern Screech-Owls combined (N = 10 per owl).

than those of males. Females also uttered notes at a significantly slower rate than did males (Table 2).

The "whinny" song has been described as a "quavering whistle (monotone or descending)" (Robbins et al. 1983:174). Typically, the initial part of the song exhibited a slight increase in frequency, while the latter part of the song was characterized by a gradual decrease in frequency (Fig. 1C). The last part of "whinny" songs often exhibited a series of rapid frequency modulations (Fig. 1C). One-way analysis of variance revealed significant individual differences ($P < 0.001$) for every parameter examined (Table 3).

In contrast to "bounce" songs, temporal characters generally were more variable than frequency characters in "whinny" songs (Table 3). As with "bounce" songs, coefficients of variation consistently revealed less intra- than interindividual variation in "whinny" songs.

DISCUSSION

Previous authors have suggested that the songs or calls of Eastern Screech-Owls may exhibit individual variation (Andrews et al. 1982, Lynch and Smith 1984). Weyden (1975) examined the "bounce" songs of several individuals and reported variation in the highest (maximum) frequency,

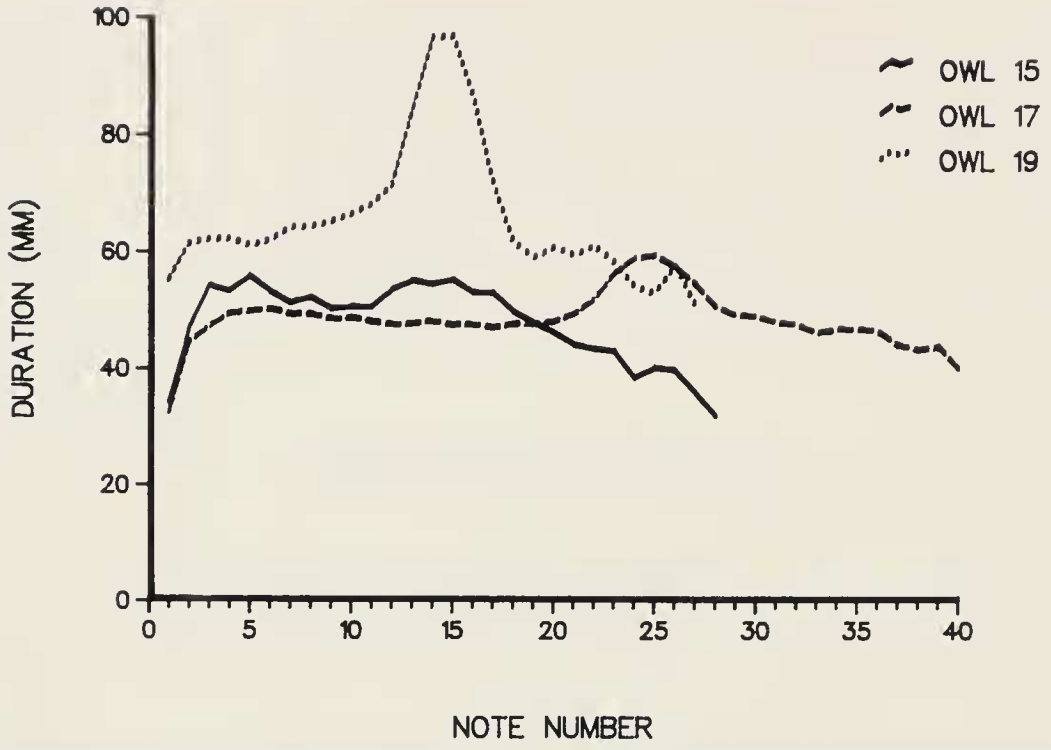

FIG. 3. Mean note durations in the "bounce" songs of three Eastern Screech-Owls (N = 10 per owl).

number of notes per second, and number of notes per motif (song). Our results are consistent with those of previous studies. Significant interindividual differences were noted in every parameter of "bounce" and "whinny" songs examined, and significant differences were also noted between the "bounce" songs of males and females. Temporal variables appeared to be more variable among individuals than the frequency variables. Variation in the duration of "bounce" songs (and, therefore, in the number of notes per song) may in part be correlated with level of "excitement." Owls generally uttered more notes per song after "bounce" songs were played back for at least five min than they did in response to playbacks of shorter duration (Cavanagh 1986).

The "bounce" songs of male and female Eastern Screech-Owls differ in frequency, with the songs of females being higher in pitch. Such differences have been noted by previous investigators (Miller 1934, Weyden 1975). This difference may allow owls to determine quickly the sex of singing conspecifics. "Bounce" and "whinny" songs also exhibited much interindividual variation, with certain features being more variable than others. Relatively stereotyped features may be useful for species recognition, while more variable features may be important for individual recognition (Falls 1982). Our analysis revealed several features of "bounce" and "whinny" songs that would appear to exhibit sufficient variation to

TABLE 2

VARIATION IN "BOUNCE" SONGS OF MALE AND FEMALE EASTERN SCREECH-OWLS

Variable	Males[a]		Females[b]		*F* ratio	*P*
	Mean	CV	Mean	CV		
Song duration (sec)	2.14	12.22	2.72	16.16	39.66	<0.001
Notes/song	30.79	11.36	33.89	8.53	7.58	<0.05
Notes/sec	14.42	3.62	12.54	7.99	202.75	<0.001
Initial frequency[c]	717	5.33	825	8.03	100.36	<0.001
End frequency	720	5.56	800	5.16	77.21	<0.001
Minimum frequency	709	5.60	795	5.64	78.98	<0.001
Maximum frequency	739	4.19	839	7.16	121.65	<0.001
Frequency range	33	39.93	46	31.09	8.81	<0.05
Mean frequency	721	4.21	823	6.80	146.02	<0.001

[a] N = 5. A total of 110 songs was analyzed (range = 10–30 songs/individual for duration, notes/song, and notes/sec; 10 songs/individual for all frequency variables).
[b] N = 3. A total of 22 songs was analyzed (10, 8, and 4 songs, respectively).
[c] All frequency measurements in hertz.

allow screech-owls to determine the individual identity of singing conspecifics. Further study is needed, however, to determine if such recognition occurs and, if so, which features of these songs are involved.

The vocalizations of non-oscines have sometimes been described as variable and highly graded (e.g., Huxley and Wilkinson 1977, Mace 1981). Several investigators, however, have reported on non-oscines in which calls or songs are relatively discrete (Beightol and Samuel 1973, Miller 1978, Wooller 1978, Hand 1981, Saunders 1983, Pietz 1985, and others).

TABLE 3

VARIATION IN NINE VARIABLES OF "WHINNY" SONGS

Variable	N[a]	Minimum	Maximum	Mean	SD	CV
Song duration[b]	11	0.94	1.50	1.15	0.16	14.16
Duration (nonmodulating)	11	0	0.48	0.19	0.15	78.30
Duration (modulating)	11	0.60	1.35	0.96	0.22	22.98
Number of modulations	11	6.59	18.29	12.78	3.75	29.31
Initial frequency[c]	11	1.015	1.411	1.213	0.111	9.15
End frequency	11	0.827	1.118	0.946	0.102	10.76
Maximum frequency	11	1.199	1.680	1.420	0.135	9.44
Minimum frequency	11	0.820	1.062	0.932	0.093	9.99
Frequency range	11	0.230	0.725	0.488	0.158	32.29

[a] N = number of individuals. A total of 152 songs was analyzed (range = 4–32 songs/individual).
[b] All duration measurements in seconds.
[c] All frequency measurements in kilohertz.

Our results indicate that the songs of Eastern Screech-Owls are also discrete, exhibiting less intra- than interindividual variation. Previous authors have noted that sounds used over long distances tend to be more discrete than sounds used at short distances (Marler 1967, Morton 1982). The songs of Eastern Screech-Owls are used in long-distance communication, as are the relatively discrete vocalizations of many other non-oscines. The variable, highly graded vocalizations of non-oscines appear to be those used at short distances.

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